MIOCENE MARSUPICARNIVORES (MARSUPIALIA) FROM CENTRAL SOUTH AUSTRALIA, *ANKOTARINJA TIRARENSIS* GEN. ET SP. NOV., *KEEUNA WOODBURNEI* GEN. ET SP. NOV., AND THEIR SIGNIFICANCE IN TERMS OF EARLY MARSUPIAL RADIATIONS

by M. Archer*

Summary

ARCHER, M., (1976).—Miocene marsupicarnivores (Marsupialia) from central South Australia. *Akotarinja tirarensis* gen. et sp. nov., *Keeuna woodburnei* gen et sp. nov., and their significance in terms of early marsupial radiations. *Trans. R. Soc. S. Aust.*, **100**(2), 53-73, 31 May, 1976.

Two of Australia's oldest known marsupicarnivores, from the Etadunna Formation of the Lake Eyre Basin, are described. *Ankotarinja tirarensis* is a tiny marsupicarnivore which may be related to didelphids as well as dasyurids. Although it is much too late in time to be the actual ancestral dasyurid, it is regarded as a structural ancestor. It is also structurally ancestral to *Keeuna woodburnei*.

Keeuna woodburnei is a small marsupicarnivore which is more similar to dasyurids than is *A. tirarensis*. It resembles species of *Phascolosorex* Matschie, 1916, *Neophascogale* Stein, 1933, *Murexia* Tate & Archbold, 1937, and some *Antechinus* Macleay, 1841. More distant relationship to didelphids is suggested.

Resemblance of both of these fossil marsupicarnivores to modern New Guinean highland rainforest dasyurids rather than to more arid-adapted Australian dasyurids, is regarded as evidence suggesting that central Australia was less arid during Etadunna time than it is now.

Introduction

In 1971 W. A. Clemens, M. O. Woodburne, C. Campbell and the author recovered fossil mammal remains from a site known as Tedford Locality, on the west side of Lake Palankarinna, Etadunna Station, South Australia. These fossils come from the Etadunna Formation which is now regarded (W. K. Harris, pers. comm.) as being approximately middle Miocene in age. In 1972 M. O. Woodburne, P. Lawson, W. Head, E. Archer and the author extensively quarried and screen-washed Tedford Locality. From the concentrate, two marsupicarnivores, as well as other mammal remains, were recovered.

Stirton, Tedford, & Miller (1961) briefly describe a third marsupicarnivore from the Etadunna Formation.

Terminology of individual teeth is that used by Thomas (1887) and Archer (1974). Terminology of tooth crowns is shown in Figure 1 and follows that used by Archer (1975a). Comparisons with other marsupicarnivores are based in large part on Archer (1976b).

Specimens with prefix P are in the fossil collection of the South Australian Museum; F in the fossil collection of the Queensland Museum; UCR in the University of California at Riverside; AMNH in the Archbold Collections of the American Museum of Natural History; J and JM in the modern collections of the Queensland Museum; and WAM in the modern collections of the Western Australian Museum.

Species names of modern Australian marsupials are those employed by Ride (1970), Laurie & Hill (1954) or Archer (1975b). Other modern marsupial names are those employed by Collins (1974). Names of Cretaceous didelphids are mainly those used by Clemens (1966). Fossil marsupial names are those employed by the most recent reviewer of those particular groups.

Taxonomy

Genus ANKOTARINJA nov.

Type species: Ankotarinja tirarensis sp. nov. (by designation and monotypy).

Generic diagnosis: Differs from other Australian and New Guinean dasyurids in having, as

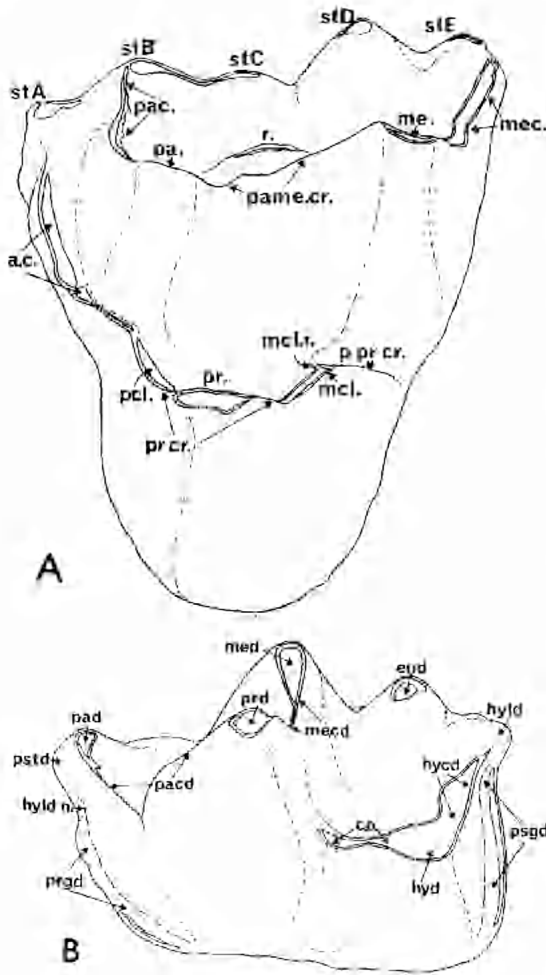* Queensland Museum, Gregory Terrace, Brisbane, Qld 4006.

Fig. 1. Terminology of molar cusps and crests (based on *Ankotarinja tirarensis*). 1A, upper molar. 1B, lower molar. *a.c.*, anterior cingulum; *c.o.*, cristid obliqua; *end*, entoconid; *hycd*, hypocristid; *hyd*, hypoconid; *hyld*, hypoconulid; *hyld n.*, hypoconulid notch; *mcl.*, metaconule; *mcl.r.*, metaconular ridge; *me.*, metacone; *mec.*, metacrista; *mecd*, metacristid; *med*, metaconid; *pa.*, paracone; *pacd*, paracristid; *pad*, paraconid; *pame. cr.*, para-metacone crest; *pcl.*, protoconule; *pprcr.*, postprotocrista; *prcr.*, protocrista; *prd*, protoconid; *prgd*, precingulid (or anterior cingulum); *psgd*, postcingulid (or posterior cingulum); *pstd*, parastylid; *r.*, ridge mesial to stC; stA-E, stylar cusps A-E.

a combination of characters, relatively unreduced talonid on $M_4^/$ with well-formed hypoconid, hypoconulid and entoconid and relatively unreduced $P_4^/$.

Origin of generic name: An allusion to *Ankotarinja*, a dreamtime ancestor (Robinson 1966,

p. 26) who, having remained buried a long time as bones in the earth, resurrected himself in a small watercourse. *Ankotarinja* is here given masculine gender.

Ankotarinja tirarensis sp. nov.
FIGS 1–5

Holotype: P18190, right dentary fragment with $M_2^/-_4$.

Type locality: Tedford Locality, Etadunna Formation, Lake Palankarinna, Etadunna Station, S.A. (28°47'S, 138°25'E).

Diagnosis: That of genus. Features likely to be of specific value include very small size, relationship of hypocristid to entoconid, size and width of anterior and posterior cingula, relative size of paraconid on $M_1^/$, and relative size of stylar cusps.

Origin of specific name: Specific name refers to the Tirari Desert, the portion of the Simpson Desert containing Lake Palankarinna.

Referred specimens: UCR, 15340, dentary fragment with $LM_1^/$; UCR, 15341, dentary fragment with $LM_2^/-_3$; UCR, 15342, dentary fragment with $RM_1^/$; F7331, dentary fragment with $LM_3^/-_4$; UCR, 15343, maxillary fragment with alveoli for $LM_2^?-_4$; UCR, 15308, $LM^{?3}$; F7332, $LM^{?3}$.

Description

Maxillary fragment (UCR, 15343) referred to this species on basis of size, has alveoli for $M_3^?-_4$ and posterior root of $M_2^?$. $M_4^/$ appears to have been as wide as $M_3^?$, presumably with relatively little reduction of protocone. $M_4^/$ length less than that of $M_3^?$, metacone root being reduced and displaced antero-lingually relative to metacone root of $M_3^?$. Zygomatic root of maxilla arises buccal to region between $M_3^?$ and $M_4^?$. Numerous small interdental fenestrae in palate between $M_2^?$ and $M_3^?$, and between $M_3^?$ and $M_4^?$.

Upper teeth represented by two isolated molars, probably $LM_2^?$ and $LM_3^?$. Although possible that these teeth actually represent $M_1^/$ and $M_2^?$, improbable for following reasons. Stylar cusps (UCR, 15308) much more reduced than those cusps on $M_2^?$ in all other dasyurids but not so strikingly reduced when compared with $M_3^?$ in some dasyurids such as *Keeuna*, described below, or some species of *Planigale* Troughton, 1928. Also, notch in antero-buccal cingulum of F7332 for reception of metastylar corner of preceeding tooth suggests F7332 is posterior molar. However, it is also true that in some dasyurids and didelphids with large $P_4^/$, such a notch sometimes exists
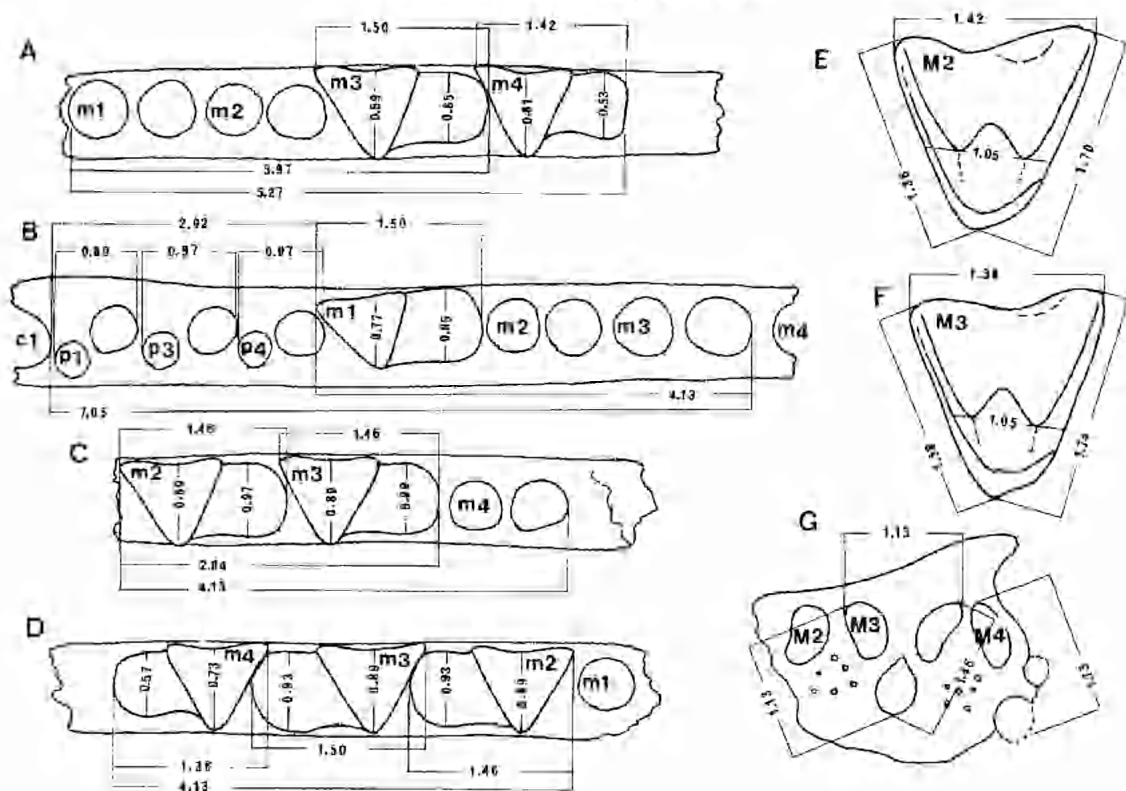
Fig. 2. Specimens of *Ankotarinja tirarensis* and their measurements (mm). A, F7331, LM$\frac{3}{4}$. B, UCR, 15340, LM$\frac{1}{4}$. C, UCR, 15341, LM$\frac{2}{4}$. D, Holotype, P18190, RM$\frac{2}{4}$. E, F7332, LM$\frac{2}{3}$. F, UCR, 15308, LM$\frac{3}{3}$. G, UCR, 15343, maxillary fragment with alveoli for M$\frac{2}{4}$.

in antero-buccal cingulum of M$\frac{1}{3}$. Probable that F7332 and UCR, 15308 represent M$\frac{2}{3}$ and M$\frac{3}{3}$ respectively rather than M$\frac{1}{3}$ and M$\frac{2}{3}$.

F7332 has at least three stylar cusps. StB connects to parastylar corner of tooth which may be distinguishable as discreet stA. Parastylar blade very short. Ectoloph crest descends gently from posterior flank stB, then rises gently, to form long low ridge-like stC. Posterior point of this cusp marked by beginning of rise in ectoloph which forms tall stD. StD has minor ectoloph crest on posterior flank which descends towards metastylar corner of tooth. Very minute rise in crest on posterior flank of stD may represent stE. Ectoloph posterior to this point very low, extending to metastylar corner of tooth. Paracone taller than stylar cusps but subequal in crown height to, or shorter than, protocone. Metacone tallest cusp. Prominent protoconule and metaconule. Ectoloph continuous on buccal edge of crown. Buccal concavity in crown outline slight. Paracrista just longer than half length metacrista. Paracrista extends from paracone to anterior

half of stB. Although slightly worn, paracrista appears to curve at buccal end to contact stB. Paracrista apparently transverse to imaginary long axis of toothrow. Para-metacrista continuous. Slight protoconule ridge may be present linking base of paracone to preprotocrista. Clear metaconular ridge present linking base of metacone to postprotocrista. Metaconular ridge extends short way up base of metacone causing bulge in base of that cusp. Metaconular ridge bounds marked declivity between posterior portion of steeply inclined postprotocrista and posterior base of metacone. Anterior cingulum complete, linking preprotocrista and antero-buccal cingulum to parastylar corner of tooth. No posterior cingulum present. Pre- and postprotocrista form large but acute angle.

UCR, 15308 has at least four stylar cusps. Possible stA as in F7332. Posterior crest from stB descends steeply to base of stC. Between stC and D, and connected by crests, another smaller stylar cusp of uncertain homology. StD small and connected to metastylar corner of

tooth by low ectoloph crest. Paracone and protocone subequal in crown height. Protoconule absent and protoconule swelling only just present. Metaconule large. Buccal concavity in crown outline deeper than in F7332. Paracrista almost three-quarters length metacrista. Paracrista worn but appears to intersect ectoloph on anterior flank of stB. No clear protoconule ridge present. Metaconular ridge small but present. Metaconular ridge does not clearly extend up base of metacone. Otherwise morphology of UCR, 15308 as in F7332.

Meristic gradients from M^2 to M^3 may be summarized as follows. Tooth length decreases. Width increases. Ectoloph becomes more evenly and deeply concave. Stylar cusps, particularly D, become smaller. Paracrista and metacrista increase in length. Para-metacrista becomes more symmetrical. Protoconule decreases in size. Angle formed by pre- and post-protocrista becomes slightly more acute. Antero-buccal cingulum increases slightly in length.

Dentary fragments indicate premolar size. UCR, 15340 has alveoli for C_1-P_3. Premolar alveoli subequal in size, indicating little or no reduction in tooth size from P_3 to P_4. P_1 presumably had posterior cingular cusp which corresponds with hypoconulid notch of M_1. P_1 anterior alveolus slightly crowded out of alignment but (as evidenced in modern species of *Planigale*. Archer 1976a), does not necessarily mean P_1 crown out of alignment. Judging from proximity of premolar and canine alveoli, premolars and canine presumably contacted one another antero-posteriorly. C_1 alveolus suggests C_1 width exceeded that of any premolar, but because of relatively unreduced P_1, C_1 probably not greatly enlarged and comparable with canine of *Ningaui* Archer, 1975b.

M_1 talonid wider than trigonid but trigonid not as compressed laterally as in most modern dasyurids. Well-developed anterior cingulum, which terminates lingually for hypoconulid notch. Parastylid corner of tooth most anterior portion of crown. Posterior cingulum comparable in length to anterior cingulum and terminates buccal to posteriorly projecting hypoconulid. Basal cingulum absent beneath postero-buccal corner of protoconid and hypoconid. Roughened enamel suggests cingulum present between base of protoconid and hypoconid. No lingual cingulum. Paraconid low, approximately same height as hypoconulid. Protoconid tallest cusp of trigonid. Metaconid just shorter than protoconid. Hypoconid just

taller than entoconid which is taller than paraconid. Paracristid complete between protoconid and paraconid but almost vertical from protoconid to shallow paracristid fissure and horizontal between paracristid fissure and paraconid. Metacristid steeply inclined on both sides of metacristid fissure. Metacristid and hypocristid approximately transverse to long axis of dentary. Cristid obliqua (damaged) extends from hypoconid to trigonid intersecting latter at point below protoconid tip, well buccal to metacristid fissure. Hypocristid extends from hypoconid to hypoconulid, without approaching entoconid. Entoconid and hypoconulid not connected by crest. Entoconid and metaconid connected by high crest.

M_2 talonid wider than trigonid. Anterior and posterior cingulum as in M_1. Buccal cingulum between protoconid and hypoconid less developed (absent in P18190). No lingual cingulum. Paraconid smallest trigonid cusp but subequal in height to hypoconid and entoconid. Metaconid much taller than hypoconid and just shorter than protoconid. Hypoconid and entoconid subequal in height. Entoconid not connected to hypoconulid by crest, but connected to metaconid as in M_1 except that crest interrupted by shallow transverse groove. Paracristid from paracristid fissure to paraconid, inclined, not horizontal. Crista obliqua extends to base of protoconid as in M_1 but anterior end appears to be distinct contribution from trigonid with slight fissure where talonid and trigonid parts meet. Trigonid portion thicker and more bulbous. Otherwise morphology M_2 as in M_1.

M_3 talonid just wider than trigonid. Anterior and posterior cingulum as in M_2. Buccal cingulum confined to area between base of protoconid and hypoconid, as thickened bulge of enamel, clearly less well-developed than anterior and posterior cingula. No lingual cingulum. Paraconid smallest trigonid cusp but taller than any talonid cusp. Entoconid not connected to hypoconulid by crest, but connected to metaconid, as in M_2. Unlike cristid obliqua in M_2, this structure in M_3 appears to lack transverse fissure separating crest into hypoconid and trigonid portions. This difference between M_2 and M_3 notable in P18190. Cristid obliqua also intersects trigonid in slightly more lingual position than in M_2. Otherwise morphology M_3 as in M_2.

M_4 trigonid wider than talonid, but talonid wider than that structure in most modern dasyurids. Anterior cingulum as in M_3. Pos-

terior cingulum absent. Buccal cingulum confined to area between protoconid and hypoconid. Paraconid just shorter than metaconid. Entoconid and hypoconid reduced relative to M_3, but larger relative to most modern dasyurids. Entoconid connected to base of metaconid via low crest. Entoconid also connected to hypoconulid by low crest. Hypocristid convex anteriorly. Hypoconulid subequal in height to entoconid. Cristid obliqua intersects trigonid base immediately buccal to point below metacristid fissure, this being markedly more lingual than similar intersection of cristid obliqua in M_3. Otherwise morphology of M_4 as in M_3.

Meristic changes along tooth row as follows. Paraconid increases in height from M_1 to M_4. Metaconid height M_1-$_4$ subequal but metaconid length at base of cusp decreases markedly from M_1 to M_3, result of reduction in size of minor crest on posterior slope of metaconid which links with entoconid. Entoconid M_1-$_3$ subequal and larger than entoconid of M_4. Hypoconulid M_1-$_4$ subequal in height and shorter than that cusp in M_4. Protoconid M_1 shorter than protoconid M_2 which is subequal to that cusp in M_3 which is larger than that cusp in M_4. Hypoconid decreases in height from M_1 to M_4. Talonid M_1-$_3$ wider than trigonid. Talonid M_4 narrower than trigonid. Paracristid M_1-$_2$ subequal and subequal to (P18190) or just shorter than (UCR, 15341) that crest in M_3. Paracristid M_4 shorter than that of M_3. Metacristid increases in length from M_1 to M_3. Metacristid M_4 shorter than metacristid M_3. Cristid obliqua intersects trigonid in progressively more lingual position from M_1 to M_4. Hypocristid M_1-$_3$ subequal in length and longer than hypocristid M_4. Anterior cingulum decreases in length slightly from M_1-M_4. Posterior cingulum M_1-$_3$ subequal in length (absent in M_4).

Discussion and comparison

Ankotarinja is a metatherian because it has four molars, a large stylar shelf, and an approximated entoconid and hypoconulid. It is also a marsupicarnivore because it has tribosphenic molars lacking hypocones.

Dental characteristics of known dasyurids, peramelids, thylacinids, didelphids, and related marsupicarnivores have been reviewed (Archer 1976b) and, to avoid repetition, it is sufficient to point out here that *Ankotarinja* can only be regarded as either a dasyurid or didelphid. Because morphological variation of teeth exhibited by didelphids and dasyurids overlaps, only incisor number and possibly dP4 cusp number permit diagnosis at the family level. All dasyurids have three lower incisors and four upper incisors on each side, whereas almost all didelphids have four lower and five upper incisors (exceptions may include *Derorhynchus singularis* Paula Couto, 1952, species of *Eodelphis* Matthew, 1916). The premaxilla and anterior region of the dentary of *Ankotarinja tirarensis* are unknown. Therefore, this marsupicarnivore cannot at present be referred conclusively to either the Dasyuridae or the Didelphidae.

Modern and fossil didelphid subfamilies exhibit greater morphological variation than dasyurids. Most are so distinct that their mere subfamilial status has been questioned, and the reasons they are doubtfully referred to the Didelphidae are also the reasons they cannot be related to *Ankotarinja tirarensis*. Only didelphines warrant closer comparison.

Some North and South American didelphines are adequately illustrated (such as the Paleocene forms described by Paula Couto 1952, 1962, 1970) but most are not. Archer (1976b) summarizes the most striking characteristics of these forms. Only species of *Coona* Simpson, 1938, *Marmosopsis* Paula Couto, 1962, *Mirandatherium* Paula Couto, 1970, *Monodelphopsis* Paula Couto, 1952, *Derorhynchus* Paula Couto, 1952, *Ischyrodidelphis* Paula Couto, 1952, *Didelphopsis* Paula Couto, 1952, *Minusculodelphis* Paula Couto, 1962 and an M^3 listed by Paula Couto (1962) as *incertae sedis* are similar to *A. tirarensis*. Among Cretaceous didelphines, species of *Alphadon* Simpson, 1927, and *Pediomys* Marsh, 1889, warrant comparison. Modern didelphines used here for comparison include two species of *Marmosa* Gray, 1821, *M.* sp. and *M. mitis* Bangs, 1898, *Monodelphis dimidiata* (Wagner, 1847), *Metachirus nudicaudatus* (Geoffroy, 1803), *Philander opossum* Gray, 1843, and *Didelphis marsupialis* Linnaeus, 1760. Of these, species of *Marmosa*, *Monodelphis* Burnett, 1830 and *Didelphis* Linnaeus, 1758 warrant closer comparison with *Ankotarinja*.

Characters of *Ankotarinja* which are unusual among dasyurids and invite broader comparison within the Marsupicarnivora (the didelphine forms noted above) are as follows: 1, large M_4 talonid; 2, relatively uncompressed M_1 trigonid; 3, buccal position of anterior end of cristid obliqua; 4, transverse orientation of metacristid; 5, large P_4; 6, large M^4; 7, stylar
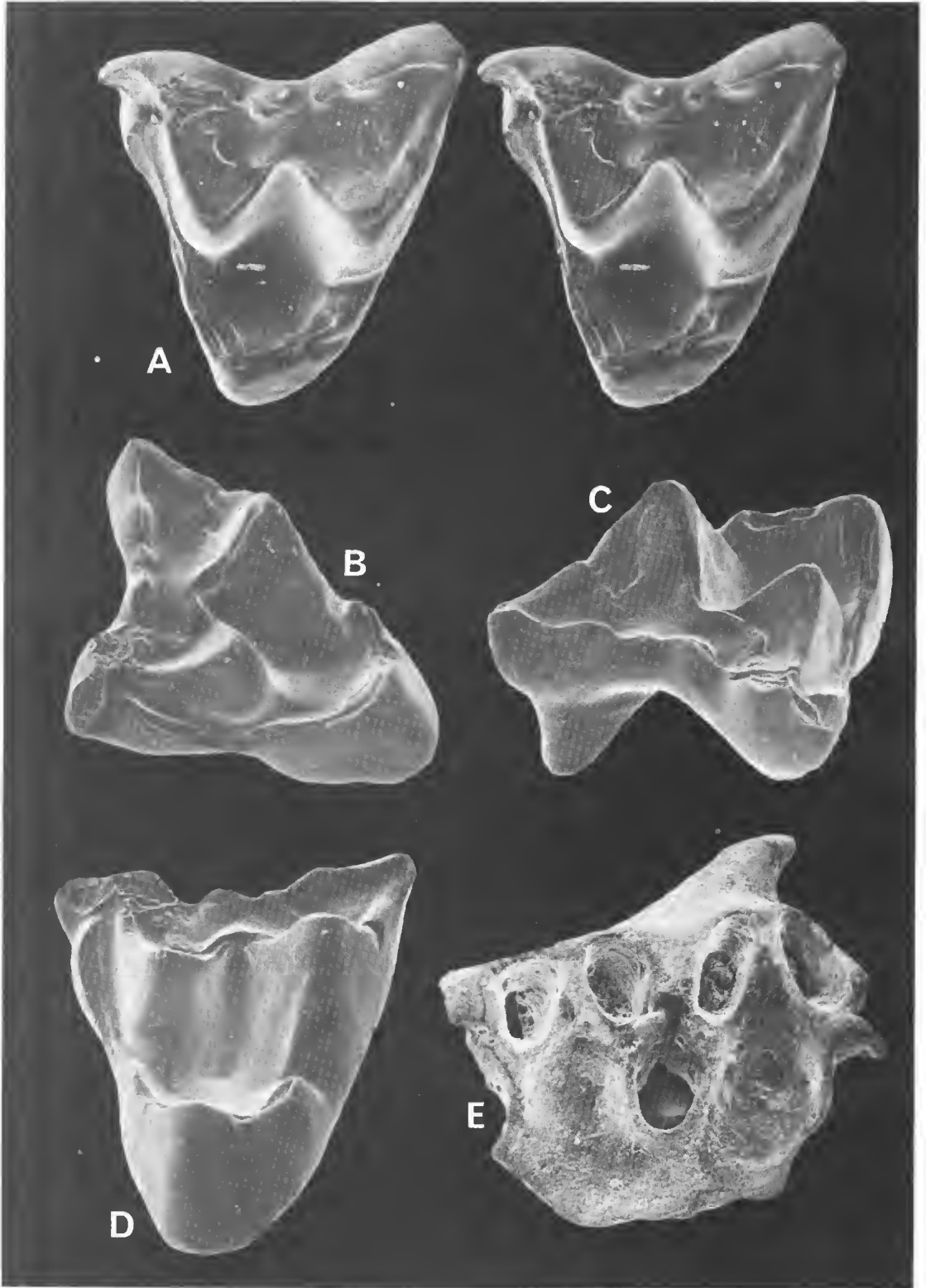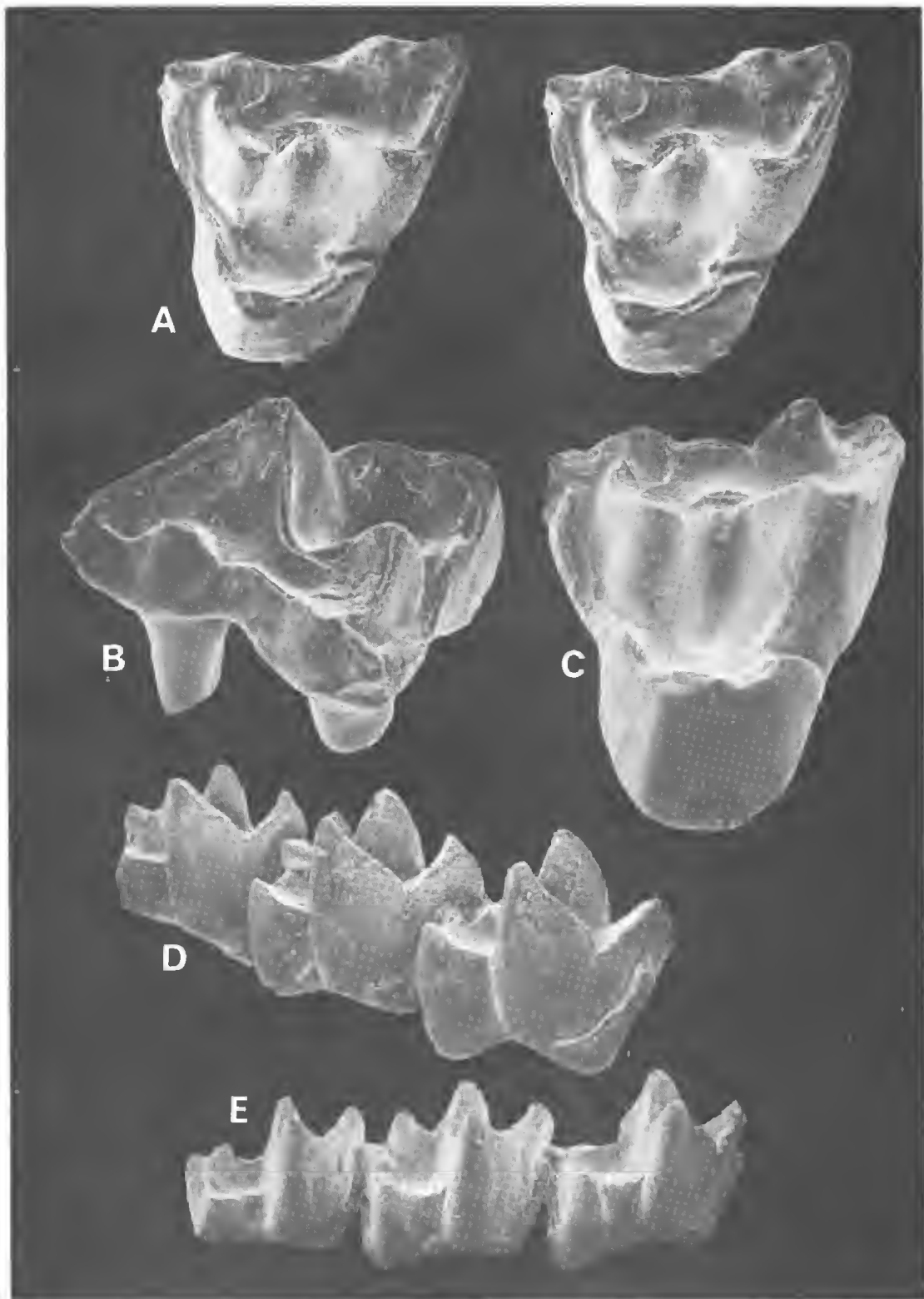
FIG. 3.

FIG. 4.

FIG. 5.

TABLE 1

Unusual characteristics of *Ankotarinia*	*Ankotarinia*	*Coona*	*Marmosopsis*	*Mirandatherium*	*Monodelphopsis*	*Derorhynchus*	*Ischyrodelphis*	*Didelphopsis*	*Minusculodelphis*	*Incertae sedis* LM₂	*Peradectes*	*Alphadon*	*Pediomys*	*Marmosa*	*Monodelphis*	*Didelphis*	*Murexia*	*Neophascogale*	*Phascolosorex*	*Sminthopsis*	*Ningaui*	*Antechinus*	*Phascogale*	*Keeuna*
1. M₄ talonid large	+	+	–	?	–	+	?	+	–	?		+	–	+	+	+	–	+	+	–	–	–	–	?
2. M₄ trigonid wide	I	?	+	+	+	+	–	+	?	?	+	+	+	+	+	+	I	I	–	–	+	–	–	–
3. C.o. buccal position	+	I	I	–	+	+	+	–	+	?	+	–	+	+	+	+	–	+	–	–	–	–	–	+
4. Transverse metacristid	+	I	I	–	–	–	–	–	+	?	+	+	+	+	+	+	–	–	–	+	–	–	–	–
5. Large P₄	+	+	+	+	I	–	–	+	+	?	+	+	+	+	+	+	+	–	–	+	–	–	–	?
6. Large M⁴	+	?	?	?	?	?	?	–	?	?	+	+	+	–	+	+	–	+	+	–	–	–	–	I
7. stD small and posterior	+	?	?	?	?	?	?	?	?	?	–	+	+	+	+	+	–	–	–	–	–	–	–	+
8. Metaconule prominent	+	?	?	?	?	?	?	+	?	?	+	+	+	–	–	–	+	+	+	–	–	+	–	+

cusp arrangement with reduced and posteriorly positioned stD; and 8, prominent metaconule. These characters are compared in Table 1 for non-dasyurid marsupicarnivores noted above, as well as dasyurids which provide the closest approximations to *Ankotarinia*. In this Table, characters 1–8 are the same as noted above. A "+" records a condition similar to or which approaches the condition found in *Ankotarinia*. A "?" indicates either that the requisite part of the dentition is unknown or not adequately preserved. A "—" indicates a character condition unlike that in *Ankotarinia*. In some genera noted, some species may be similar to, while others differ from, the condition in *Ankotarinia*. In this case, a "+" only is recorded.

M₄ and M⁴ size

Large M⁴ and M₄ talonid are related characters and more common among structurally ancestral didelphines than dasyurids. Very few dasyurids have the M₄ talonid as relatively large as it is in *Ankotarinia*. The M₄ talonid of most dasyurids is laterally compressed with one or at most two cusps present, the hypoconid and entoconid or hypoconid and hypoconulid. In this character, *Ankotarinia* is most similar (among dasyurids) to *Neophascogale* and to a lesser extent *Phascolosorex*. Three distinct cusps may sometimes be present on the M₄ talonid of other dasyurids

such as *Murexia*, *Myoictis* Gray, 1858 and some *Antechinus* but in these forms the M₄ trigonid is relatively larger than in *Ankotarinia*, while the talonid is transversely compressed. Relatively large M₄ talonids characterize many didelphine groups. For example, the talonid of M₄ in *Marmosa* is only slightly more reduced than that of *Ankotarinia*. However, in *Marmosa* the whole M₄ is not as reduced relative to M⁴ as it is in *Ankotarinia*. *Philander* Brisson, 1762 (J3460), and *Metachirus* Burmeister, 1854 (J3461) also show a relatively unreduced M₄ talonid. *Coona* and *Guggenheimia* Paula Couto, 1952 have M₄ talonids even wider than the trigonids. Extremely narrow M₄ talonids (comparable with the condition in most dasyurids) are found among didelphines in species of *Minusculodelphis* and and *Marmosopsis*.

Overall reduction of M₄ relative to M₃, such as occurs in *Ankotarinia*, does not occur in any modern dasyurids. It is common only to some didelphoids. M⁴ of *Ankotarinia* is unknown but maxillary fragment UCR, 15343 indicates that this tooth was as wide but not as long antero-posteriorly as M⁴ of most didelphids. It was comparable in length to M⁴ of some modern dasyurids such as *Neophascogale*, but wider than that tooth in most modern dasyurids. Size of M⁴ in modern dasyurids

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Fig. 3. *A–E*, scanning electron microscope photographs of *Ankotarinia tirarensis*. *A–D*, UCR, 15308, LM³. *A*, stereophotographs. *E*, UCR, 15343, maxillary fragment with alveoli for LM³–⁴.

Fig. 4. *A–E*, scanning electron microscope photographs of *Ankotarinia tirarensis*. *A–C*, F7332, LM³. *A*, stereophotographs. *D–E*, Holotype, P18190, RM₃–₄, entoconid broken off RM₄.

Fig. 5. *A–E*, scanning electron microscope photographs of *Ankotarinia tirarensis*. *A–B*, UCR, 15340, dentary fragment with LM₂–₃. *D*, UCR, 15341, dentary fragment with LM₂–₄. *E*, F7331, dentary fragment with LM₃–₄.

appears to be related to relative length of the cheek-tooth row, being shorter and more reduced in forms with more compressed tooth rows. This compression commonly occurs in more strictly carnivorous forms where emphasis is on development of metacrista-paracristid shearing elements. In more insectivorous forms, paracrista-metacristid shearing elements are relatively less reduced, resulting in a relatively more functional M^3 paracrista and larger M_1 talonid.

Reasons for overall reduction of M_1 relative to M^3 are not easy to interpret. In some diprotodont marsupials where reduction of M_4 is advanced, sometimes even involving loss, P_4 is developed as a large sectorial or even plagiaulacoid tooth, possibly reflecting a shift anteriorly in shearing emphasis, reducing the importance of M_4. In *Ankotarinja*, although P_4 is large, the size is not particularly different from that of some didelphines which lack a reduced M_1.

M_1 trigonid width, paraconid reduction, and size of P_4

Reduction of the M_1 paraconid and P_4 are related characters and often accompanied by transverse compression of the M_1 trigonid and increase in relative importance of the protoconid. The relatively large P_4 and wide trigonid of M_1 in *Ankotarinja* are unmatched among living dasyurids. Even in *Neophascogale* the M_1 trigonid is transversely compressed with gross reduction of the paraconid. In *Ankotarinja* the M_1 paraconid is very low on the trigonid but not strongly deflected out of alignment with the other lingual cusps such as occurs in most dasyurids. The closest match among dasyurids is found in species of *Sminthopsis*, *Murexia*, and *Keeuna* but even here, the M_1 paraconid is shifted anteriorly relative to that cusp in *Ankotarinja*. A relatively wide trigonid on M_1 occurs in most didelphoids, and in part, reflects the relatively large P_4 in most of these forms. In dasyurids which show premolar reduction, it is P_1 which is reduced or lost in the lower dentition (including the interesting case of *Planigale gilesi* Aitken, 1972; Archer 1976a), while in didelphoids and borhyaenids it is P_1 which is normally reduced. The only marked exception are species of *Zygolestes* Ameghino, 1898, which are unique among didelphids in having an extremely reduced, although two-rooted, P_4. Reig (1957) notes that in the M_1 the paraconid is more buccal in position than is normal for the group. This modification is much less than that seen

in the trigonid of dasyurids with a comparably reduced P_1. Reduction of P_4 normally occurs among dasyurids which exhibit a compressed cheek-tooth row, increased carnassiality as judged by proportionate increase in metacrista-paracristid length, enlarged canines, etc. (Archer 1976b). Attendant reduction of the M_1 paraconid and increase in size of the M_1 protoconid shift the premolariform-molariform boundary posteriorly. The M_1 trigonid functions as a stabbing, piercing premolar rather than a sectorial trigonid. Further, in dasyurids which have lost P_4, such as *Dasyurus* Geoffroy, 1796 and *Sarcophilus*, the metacrista-paracristid length of M^3 is greater than that of M^2 or M_1. The net effect is to concentrate the sectorial function of the molars at a point posterior of the middle of the molar row. Posterior shift of the premolariform-molariform boundary may be seen in this way as merely maintaining the structurally ancestral relationship between these two types of teeth.

Ankotarinja is clearly structurally ancestral in this regard and more similar to didelphids than dasyurids.

Position of the cristid obliqua

The M^3 cristid obliqua of *Ankotarinja tirarensis* is unlike almost all dasyurids in that it intersects the trigonid at a point so far buccal to the metacristid carnassial notch. This condition is approached in *Neophascogale* and to a lesser extent in *Keeuna*, while in other dasyurids the cristid obliqua tends to intersect the trigonid just buccal to the carnassial notch. In some dasyurids (e.g. *Neophascogale* and *Dasyurus*) the protoconid flank contributes to the cristid obliqua on M_{1-3}, and this same condition occurs in *Ankotarinja*, at least on M^3. Clemens (1966) suggests that lower teeth (except perhaps dP_4) of pediomyids can be distinguished from species of *Alphadon* in that the crista obliqua in pediomyids intersects the base of the trigonid well buccal to the metacristid fissure. This pediomyid condition is also present in all modern didelphids examined in the present study and appears to be present in illustrations of species of many of the South American fossil didelphines. The condition in *Ankotarinja* is closer to this pediomyid and didelphine condition than it is to most modern dasyurids or *Alphadon*.

Although the functional significance of this difference is not clear, a relatively more buccal position produces a larger talonid basin. Position of the cristid obliqua must also reflect position of the paracone, a more buccal position

indicating a relatively reduced or more buccally situated paracone.

The condition found in *Ankotarinja* and some dasyurids (e.g. *Dasyurus*) of a small anterior component of the cristid obliqua formed by the protoconid flank results in the development of a small accessory carnassial notch against which shears the paracone. This makes an effective point-cutting unit that supplements those developed on the trigonid.

Transverse metacristid

In *Ankotarinja* the metacristids are transverse to the long axis of the dentary. In dasyurids, this condition is present only in species of *Sminthopsis, Antechinomys* Krefft, 1867, and to a lesser extent, species of *Ningaui* and some species of *Planigale*. In other dasyurids, the metaconid is displaced posteriorly relative to the protoconid resulting in the metacristid and paracristid forming a more obtuse angle. The transverse condition is present among some but not all modern didelphines, some Cretaceous didelphoids, and many Tertiary didelphids.

Among dasyurids, markedly non-transverse metacristids occur only in the more carnivorous forms. This structural trend is noted by Bensley (1903) who regards it as modification towards longitudinal and away from transverse shear. In this respect, the lower molars of *Ankotarinja* demonstrate the structurally primitive insectivorous condition, which is more common among didelphids.

Stylar cusp size and position

Terminology of the stylar cusps of *Ankotarinja* used here is set out elsewhere (Archer 1976b).

The stylar cusp condition in *Ankotarinja* is closer to that of didelphids than dasyurids in having a large stylar cusp posterior to stB, anterior to stD and buccal to the low point in the para-metacrista of M³, which is the homologue of the normal didelphid and variably present, but invariably small, dasyurid stC. Further, stD in *Ankotarinja* is smaller and slightly more posterior in position than that cusp in modern dasyurids. These non-dasyurid-like features are common among Cretaceous didelphines such as glasbiines, some species of *Alphadon* and *Pediomys*.

Stylar cusps do not have occlusal counterparts in lower molars, yet they clearly sustain wear. This wear must result from food abrasion during initial puncturing prior to the cutting or shearing occlusal phase. As the dentary closes, force is applied to food trapped between teeth

by the lower molars in opposition to the whole of the upper molars including the stylar shelf. The area of the crushing or puncturing surface is increased by larger stylar cusps. In marsupicarnivores, stylar cusp reduction occurs in the more carnivorous forms such as *Sarcophilus, Thylacinus* Temminck, 1824, and borhyaenids where perhaps the puncturing value of these cusps is overshadowed by the need to have large and sturdy shearing crests. The stylar cusp size and arrangement in *Ankotarinja* may therefore be interpreted as evidence for insectivorous rather than carnivorous habits.

Metaconule development

In *Ankotarinja* the metaconule of the upper molars is a prominent feature, while the protoconule is not present in M³. Conule development is present in some dasyurids and many didelphids. It is well-developed in most Cretaceous didelphines where both protoconules and metaconules occur. Simpson (1928) notes that these cusps in recent didelphids are represented at most by vestiges.

The possible functional significance of metaconules is discussed elsewhere (Archer 1971). In addition, well-developed metaconules may serve as shearing counterparts for the hypoconid and buccal edge of the hypocristid.

Summary

The dentition of *Ankotarinja* resembles that of many didelphids, and some dasyurids such as *Neophascogale, Murexia,* and *Sminthopsis.* Because of the middle Miocene age of the deposit, as well as the fact that two relatively more modern-type dasyurids (*Keeuna* and an unnamed form noted by Stirton, Tedford, & Miller 1961) are in the same deposit, it would be absurd to regard *Ankotarinja* as the ancestral dasyurid. However, it does preserve characters which could be regarded as structurally ancestral to modern dasyurids. It is clear that many South American Tertiary didelphines of Paleocene age (Graham & Ride 1967) share characters with *Ankotarinja* which it does not share with modern dasyurids. Taking into account all available morphological characters together with what is currently known of their distribution, and recognizing that the characters (incisor number and dP4 morphology) which will distinguish between the two lineages Dasyuroidea and Didelphoidea are not preserved, one cannot avoid concluding that the data available indicate a marsupicarnivore, probably belonging to the Dasyuroidea, but which, like the slightly older phalangeroid *Wynyardia* Spencer, 1900 (Ride 1964b), also

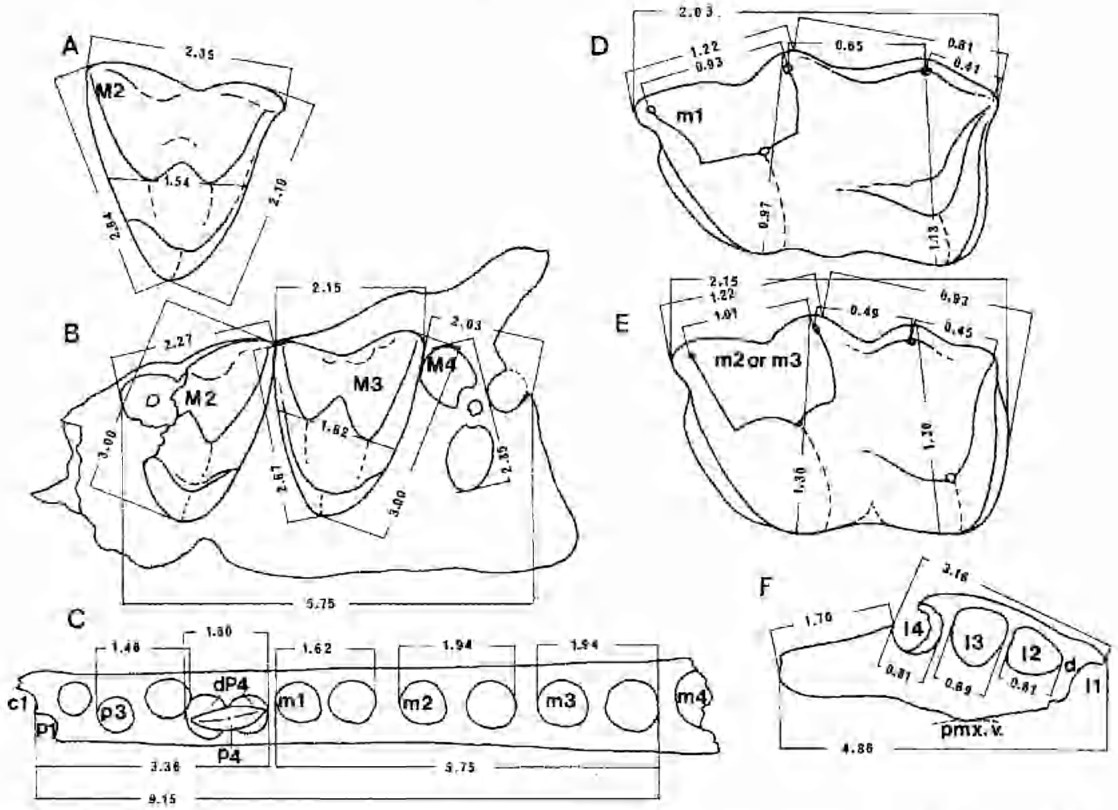Fig. 6. Specimens of *Keeuna woodburnei* and their measurements (mm). *A*, Holotype, P18191, RM$\frac{2}{2}$. *B*, F7333, maxillary fragment with LM$\frac{2}{2}$ (broken), LM$\frac{3}{3}$ and alveoli for LM$\frac{4}{4}$. *C*, UCR, 15346, dentary fragment with LP$\frac{4}{4}$ erupting and alveoli for LC$_1$-M$_4$. *D*, F7334, LM$\frac{4}{4}$. *E*, UCR, 15344, LM$\frac{2}{2}$ or M$\frac{3}{3}$. *F*, tentatively referred to *K. woodburnei*, UCR, 15347, premaxillary fragment, with alveoli for RI$\frac{1-4}{2}$: d represents diastema between alveoli for RI$\frac{1}{2}$ and RI$\frac{2}{2}$; pmx.v. represents edge of premaxillary vacuity.

retains a number of characters of a sort which reveals its derivation from early Tertiary didelphoids or the didelphoid-dasyurid stem. If it should be discovered that *Ankotarinja* possesses a didelphoid incisor number, the author will have no hesitation in describing it as a didelphoid with characters foreshadowing dasyurids, but it is clear that it is far too late in time to be an ancestor to the whole dasyurid family. For the present, it is listed as ?Dasyuridae.

Genus KEEUNA nov.

Type species: Keeuna woodburnei sp. nov. (by designation and monotypy).

Generic diagnosis: Differs from other Australian and New Guinean dasyurids including *Ankotarinja* in combining relatively reduced stD on M$\frac{2-3}{}$, large M$\frac{4}{}$, antero-posteriorly shortened M$\frac{3}{}$, and virtually absent posterior cingulum on M$\frac{2-3}{}$ (although mild posterior

cingular swelling present on holotype), and relatively unreduced P$\frac{4}{4}$.

Origin of generic name: Kee, central Australian Aboriginal word for wild cat; *una,* central Australian Aboriginal word for forgotten (Smith 1880). *Keeuna* is here given masculine gender.

Keeuna woodburnei sp. nov.

FIGS 6–8

Holotype: P18191, isolated RM$\frac{2}{2}$.

Type locality: Tedford locality, Etadunna Formation, Lake Palankarinna, Etadunna Station, S.A. (28°47'S, 138°25'E).

Diagnosis: That of genus. Relative development of entoconids, stylar cusps, and size may prove to be diagnostic species characters.

Origin of specific name: The specific name is in honour of Dr M. O. Woodburne who helped

find all of the material referred to this species and who, with Dr W. A. Clemens, gave the author his first opportunity to study Australian Tertiary fossils.

Referred specimens: UCR, 15271, RM^3; F7333, left maxillary fragment with M^3 and part of M^2; UCR, 15347, right premaxillary fragment; UCR, 15344, isolated LM_4; UCR, 15348, left dentary fragment; UCR, 15286, trigonid RM_1; UCR, 15269, trigonid RM_4; UCR, 15274, isolated M_2; UCR, 15345, left dentary fragment; UCR, 15346, dentary fragment with LP_4 erupting; F7334, isolated LM_4.

Description

Maxillary fragment (F7333) has LM^3, posterior part LM^2, and alveoli for LM^1. M^1 narower than M^3 but relatively little reduced antero-posteriorly, being only slightly shorter than M^3. Metacone root M^1 large, equivalent in size to protocone root, and only just smaller than paracone root. Interdental fenestrae occur between M^2 and M^3 and between M^3 and M^4. Maxillary root of zygomatic arch arises buccal to M^3-^4. Infraorbital canal opens on anterior edge of maxillary fragment, dorsal to anterior end M^2.

Premaxillary fragment (UCR, 15347) may represent *K. woodburnei* on basis of size, because larger than would be expected for other known Ngapakaldi forms. Four alveoli present. Largest represents RI^1 (alveolus broken). This alveolus separated from alveolus for RI^2 by very short diastema. Alveoli for RI^2-^3 contact one another. RI^1 alveolus inclined posteriorly and suggests RI^1 inclined antero-ventrally. Based on alveolar size, RI^1 largest incisor, RI^2 exceeded RI^4 in length which exceeded RI^3 in length. This may be misleading since posterior lobe of RI^4 (occurrence of which is not uncommon among modern dasyurids) may have caused this tooth to be longer than RI^2. Also, root for RI^1 commonly large in modern dasyurids, while crown may be very reduced. Posterior to RI^1 alveolus, premaxillary wall descends into pit which is occlusal counterpart of RC_1, indicating RC_1 large and caniniform.

M^2 with continuous anterior cingulum connecting parastylar corner of tooth to preprotocrista (piece of enamel missing from anterior cingulum of holotype). Posterior cingulum absent (F7333) to doubtfully present (P18191) as swelling at base of crown above metacone root. Swelling not continuous with postprotocrista whereas this is the case in modern dasyurids with undoubted posterior cingula. Five distinct buccal cusps present. StA

occurs at buccal end of anterior cingulum, between parastylar corner of tooth and stB. Almost vertical, minor crest connects stA to parastylar corner of tooth, that part of tooth which would overlap postero-buccal edge of P^3. Very minor, more gently inclined crest conects stA to stB. StB connected to paracone by long paracrista. Buccal crest extends posteriorly from stB to contact small, low stC which is adjacent to another small low stylar cusp of uncertain homology. These two stylar cusps not connected by crest. The posterior small cusp connects to larger stD by minor, inclined crest. StD largest stylar cusp, but smaller than that cusp in M^2 of modern dasyurids. StD connects to metastylar corner of tooth by long, low crest. No evidence of stE. From metastylar corner of tooth, three crests radiate: buccal crest to stD; metacrista to metacone; and minor short crest that extends antero-lingually from metastylar corner and ends within short distance of tooth corner. Crescentic enamel ridge occurs lingual to midpoint of ectoloph, and buccal to mid-point of para-metacrista. Ridge may represent cusp analogous to similar structure in some specimens of *Sminthopsis virginiae* Tarragon, 1847. Paracone shorter than metacone, and two cusps widely separated. Small but clear metaconular ridge extends from base of metacone to middle of postprotocrista. Postprotocrista terminates as steep-sided crest adjacent to base of metacone. Deep pyramid-shaped fossa exists between bases of paracone and metacone and buccal flank of protocone. Metacrista approximately 1.5 times length paracrista. Ectoflexus in ectoloph slight, point of inflection immediately posterior to stC.

M^3 with continuous anterior cingulum. Posterior cingulum absent. At least four stylar cusps present. Parastylar extension of tooth small and accordingly little overlap of metastylar corner of M^2 occurs. StC connected to stB as in M^2. On anterior flank of cusp called stC (F7333), small, possibly distinct swelling occurs which may be homologous with stC of M^2. If so, cusp posterior to that cusp in M^2 might be homologous with single conspicuous cusp in this position on M^3. Posterior to stC of M^3 is slightly larger stD. Posterior to stD, and connected to it by crest, is stE. This cusp extends posteriorly as ridge which terminates short of metastylar corner of tooth. Only metacrista radiates from metastylar corner of tooth. Lingual to stC, as in M^2, crescentic ridge occurs which may be distinct cusp. In addition

TABLE 2

Unusual characters of *Keeuna*	*Keeuna*	*Ilidelphopsis*	*Peradectes*	*Alphadon*	*Pediomys*	*Marmosa*	*Monodelphis*	*Didelphis*	*Murexia*	*Neophascogale*	*Phascolosorex*	*Sminthopsis*	*Ningaui*	*Antechinus*	*Ankotarinja*
1. Large M⁴	+	+	±	+	+	+	+	±	−	+	±	−	−	−	+
2. Mx lack post. cing.	+	+		+	−	+	+	+	−	−	−	+	+	+	+
3. Small stD	+	+	+	±	+	+	+	−	−	−	−	−	−	−	+
4. Compressed M³	−	−	−	−	+	÷	+	−	+	−	−	−	+	+	−

to metaconular ridge, as in M³, clear meta-conular swelling present on postprotocrista. No clear protoconule or protoconular ridge present. Metacrista less than 1.5 times length paracrista. Ectoflexus M³ broad and relatively deep. Point of inflection in ectoflexus occurs anterior to stC. Otherwise morphology of M³ as in M³.

Dentary with two branches of inferior dental canal, one emerging at point level with middle of M₁ on buccal surface of dentary while other emerges at point beneath posterior root P₁ (latter condition determined from juvenile dentary, UCR, 15346). UCR, 15346 only specimen with premolar alveoli preserved. P₁ erupting in this specimen. As result, apparently crowded premolar condition may become less crowded in adult dentary. Premolar gradient suggested by alveoli; P₁ shorter than P₃ which is subequal in length to P₄. DP₄ alveoli suggest tooth as large as P₄ and two-rooted. P₄ alveoli acutely oblique with anterior root postero-buccal to C₁ alveolus. Posterior root P₄ immediately posterior to C₁ alveolus. P₃ and dP₄ alveoli suggest teeth only mildly out of alignment (although crown alignment need not be reflected in root alignment). C₁ alveolus relatively small, suggesting tooth no wider than P₃.

P₄ partly erupted and partly obscured. Tooth single-cusped with tall protoconid. Paracristid steep. No anterior cingulum cusp. Metacristid more gently inclined and appears to directly contact very small posterior cingulum cusp. No buccal or lingual cingula evident.

M₁ talonid wider than trigonid, and trigonid more laterally compressed than that structure in *Ankotarinja*. Anterior cingulum relatively well-developed, terminating lingually with hypoconulid notch, and terminating buccally anterior to buccal base of protoconid. Posterior cingulum slightly shorter than anterior cingulum and extends to contact hypoconulid. Pronounced cingulum development, as bulge

between bases of protoconid and hypoconid. No lingual cingulum. Paraconid low on crown, approximately same height as entoconid. Protoconid tallest trigonid cusp. Metaconid just shorter than protoconid. Hypoconid subequal to entoconid in height. Paracristid complete between protoconid and paraconid, and anterior part of crest steeply inclined. Metacristid and apparently paracristid fissures extend below cutting edges of crests. Crest descends from posterior wall of metaconid and meets crest from anterior wall of entoconid. Two crests meet with shallow, open fissure. Crest development from posterior wall of entoconid slight to absent. No crest links entoconid and hypoconulid. Hypocristid extends postero-lingually from hypoconid to hypoconulid. Both hypocristid and metacristid clearly not transverse to long axis of tooth. Cristid obliqua intersects trigonid well buccal to point below metacristid fissure.

Isolated molars posterior to M₁ not been positively identified. UCR, 15274 and UCR, 15344 tentatively regarded as representing M₂ and M₃ respectively. This conclusion based on trigonid width and paraconid height. Both increase posteriorly in most modern dasyurids between M₁ and M₃.

UCR, 15274, LM₂, trigonid just narrower than talonid. Hypoconulid notch between parastylid and lingual end of anterior cingulum larger than in M₁. Cingulum development between base of protoconid and hypoconid does not produce buccal convexity in crown outline. Paraconid higher on crown than in M₁. Paracristid fissure well-developed below crest. Cristid obliqua intersects trigonid and extends short way up trigonid wall at point lingual to point of same intersection in M₁. Otherwise morphology UCR, 15274 same as M₁.

UCR, 15344, LM₃, trigonid and talonid subequal in width. Hypoconulid notch larger than in M₁ but subequal to that of M₂. Posterior

cingulum less convex posteriorly than in M_1^4 or M_2^4. Also, posterior cingulum extends lingually and contacts hypoconulid rather than stopping short of it as in M_1^4 and M_2^4. Basal cingulum between protoconid and hypoconid well-developed but does not cause buccal convexity. Crests linking metaconid and entoconid less-developed than in M_1^4 and M_2^4 (although M_3^4 damaged in this region). Cristid obliqua intersects trigonid as in M_2^4. Otherwise morphology M_3^4 as in M_1^4.

Discussion and comparison

A summary of important dental characters in marsupicarnivores in general is given elsewhere (Archer 1976b) and to avoid repetition, discussion of dental characters of *Keeuna* is largely restricted to those characters which either make *Keeuna* unusual among the Dasyuridae or suggest affinities outside of that family. Comparison within the Marsupicarnivora is restricted to the Dasyuridae and Didelphidae, because no other families contain forms even remotely similar to *Keeuna*.

Keeuna cannot be referred conclusively to the Dasyuridae for the same reasons given above in the discussion of *Ankotarinja*. However, the features of *Keeuna* are more suggestive of known dasyurids than didelphids. If the referred premaxilla does in fact represent *Keeuna*, there is no reason to doubt its reference to the Dasyuridae. This specimen shows alveoli for four incisors. The diastema behind the anterior alveolus confirms that the anterior alveolus represents I^1. No dasyurid or didelphid known to the author has a diastema within the incisor row posterior to I^1 or anterior to I^4, other than a variably present diastema between I^1 and I^2.

Although the dental characters of *Keeuna* are all present in one dasyurid or another, considered together: 1, the large M^4 (inferred from alveoli); 2, virtual lack of a posterior cingulum on the upper molars; 3, relatively reduced stD on M^3; and 4, antero-posteriorly shortened M^3; they make *Keeuna* unique among dasyurids. These characters are compared in Table 2 for didelphids and dasyurids which provide the closest similarities in upper molar morphology to *Keeuna*. Many South American Tertiary didelphids which have a lower molar morphology (e.g. *Mirandatherium*, Paula Couto 1962, fig. 4) similar to that of *Keeuna*, are unrepresented by upper molars and not included in Table 2. Characters 1–4 are the same as noted above. A "+" records a condition similar to or closely approaching that

found in *Keeuna*. A "?" indicates either that the dentition is too incomplete or poorly preserved to enable determination. A "—" indicates a condition unlike that in *Keeuna*. Polytypic genera which have some forms similar to but others differing from *Keeuna* are recorded only as "+". M^x indicates any or all upper molars.

M^4 size

The possible significance of a large M^4 is discussed above. *Keeuna* exhibits similarities in this regard to many didelphids but only a few structurally ancestral dasyurids, including *Ankotarinja*.

Posterior cingula on upper molars

Elsewhere (Archer (1976b) it has been noted that cingula have the effect of increasing molar surface area. It is also possible that posterior cingula on upper molars act as supplementary shearing crests in opposition to the paracristids which come into effect after the paracristids shear past the metacrista. Distribution of this character in modern dasyurids (Archer 1976b) does not appear to lend itself to phylogenetic interpretation, being present in some but not other species of single genera such as *Antechinus*. Absence in *Keeuna*, although perhaps phylogenetically unimportant, is useful in combination with other characters for differentiating the genus.

Stylar cusp D

Small size of this cusp allies *Keeuna* with *Ankotarinja*, as well as with many didelphids. The possible significance of stylar cusp size is discussed above in regard to *Ankotarinja*.

Compressed M^3

M^3 of *Keeuna* is longitudinally compressed in comparison with structurally ancestral dasyurids such as *Neophascogale* but not in comparison with structurally derived dasyurids such as *Sminthopsis* whose molars are even more compressed. Bensley (1903) notes relative compression in some dasyurids and regards this as a more insectivorous than carnivorous adaptation. Extremes of non-compression, such as occur in *Sarcophilus*, result in shearing crests which approach longitudinal rather than a transverse orientation.

Detailed comparisons

Overall, *Keeuna* more closely resembles some dasyurids including *Phascolosorex*, *Neophascogale*, some *Antechinus*, *Murexia*, and *Ankotarinja*, than it does didelphids. Particular similarities and differences are noted below.

Similarities which extend to all dasyurids are not noted.

Phascolosorex: Similarities include relatively large $M^{\frac{4}{4}}$ and metaconule. Upper molars of *Keeuna* differ from those of *Phascolosorex* (e.g. AMNH, 109758, 151992, 101975 and 109757) in that stylar cusps much closer to buccal edge of crown; small stylar cusp occurs lingual to stC (although in some specimens of species of *Phascolosorex* such as AMNH, 151992, this cusp suggested on M^{3}); M^{3} shorter antero-posteriorly; paracrista and metacrista enclose more acute angle; and M^{1-4} lack clear posterior cingula. In lower molars of *Keeuna*, trigonid and paraconid of M^{4} much less reduced; crests from posterior face of metaconids much better-developed; talonid M^{4} relatively slightly wider.

Neophascogale: Large $M^{\frac{4}{4}}$ of *Keeuna* similar to that of *Neophascogale* (e.g. AMNH, 109524). Differences in upper molars of *Keeuna* include those noted above in comparison with *Phascolosorex* as well as lack of distinct antero-lingual low crest developed on base of protocone (which has nothing to do with preprotocrista); ectoloph and para-metacrista relatively more widely separate at their closest point; protoconule slightly better-developed. Lower molars *Keeuna* differ in having less reduced M^{4} trigonid; relatively shorter, wider molars; cristid obliqua which intersects trigonid in relatively more lingual position (notable in M_{2-4}); lack of post-entoconid crest which directly connects to hypoconulid; relatively lower talonids, higher trigonids; relatively shorter talonids.

Antechinus: Resemblance with some *Antechinus* (e.g. *A. mayeri* (Rothschild & Dollman, 1930), AMNH, 109816, *A.* sp., AMNH, 190877 from New Guinea, and *A. melanura* (Thomas, 1899), WAM, M5517) considerable including overall proportions of M^{2-3}; somewhat similar reduction of stD on M^{3}; relatively unreduced P^{4}. Upper molars *Keeuna* differ in that stD relatively slightly more reduced on M^{3}; stB relatively more posterior on ectoloph; all stylar cusps relatively smaller; M^{1-3} somewhat shorter antero-posteriorly; $M^{\frac{4}{4}}$ notably longer in proportion to length of M^{3}; posterior cingula absent; metacone and paracone M^{2-3}

relatively closer in height; larger, more conspicuous cusp or crest occurs lingual to stC; ectoflexus in relatively more posterior position; protocone shorter antero-posteriorly at its longest point. Lower molars *Keeuna* differ in having less-compressed trigonid on M^{4} with larger paraconid; relatively wider talonid on M^{3}; lack complete buccal cingulum such as occurs on M^{1-4} of some *Antechinus* species (e.g. *A. mayeri*); lower molars relatively shorter, wider; entoconids M_{2-3} relatively taller; hypoconulid wider and extends farther from postero-lingual corner of M_{1-3}.

Murexia: Similarities between species of *Murexia* (e.g. *M. longicaudata* (Schlegel 1866) (AMNH, 101972 and 152035)) include comparable relative length of M^{3}; relatively unreduced P^{4}. Upper molars of *Keeuna* differ in same features from *Murexia* as they do from molars of *Antechinus* except as follows. In *Keeuna*, all stylar cusps except C relatively smaller; posterior cingulum of upper molars virtually undeveloped (although only slight posterior cingular development occurs in species of *Murexia*); M^{3} relatively longer; metaconular crest from base of metacone less well-developed and lacks low, minor crest linking stD with metacone (latter observed only in unworn specimens of *Murexia* examined in this study, AMNH, 152035). Lower molars of *Keeuna* differ in same features from teeth of *Murexia* that differentiate teeth of *Antechinus*, except as follows. In lower molars of *Keeuna* entoconids relatively shorter antero-posteriorly, and higher; buccal cingulum absent (occurs in one specimen of *Murexia*, AMNH, 152035); low direct crest linking posterior face of entoconid with hypoconulid absent.

Ankotarinja: Comparison with much smaller *Ankotarinja* demonstrates that both forms similar in having relatively small stylar cusps (particularly stD); stylar cusp(s) present between B and D; no posterior cingulum; complete anterior cingulum; slightly smaller paracones than metacones; lack of direct crest linking entoconid with hypoconulid; relatively large P^{4}; unreduced trigonid and paraconid of M^{4}. Upper molars of *Keeuna* differ from those of *Ankotarinja* in larger size and more anterior position
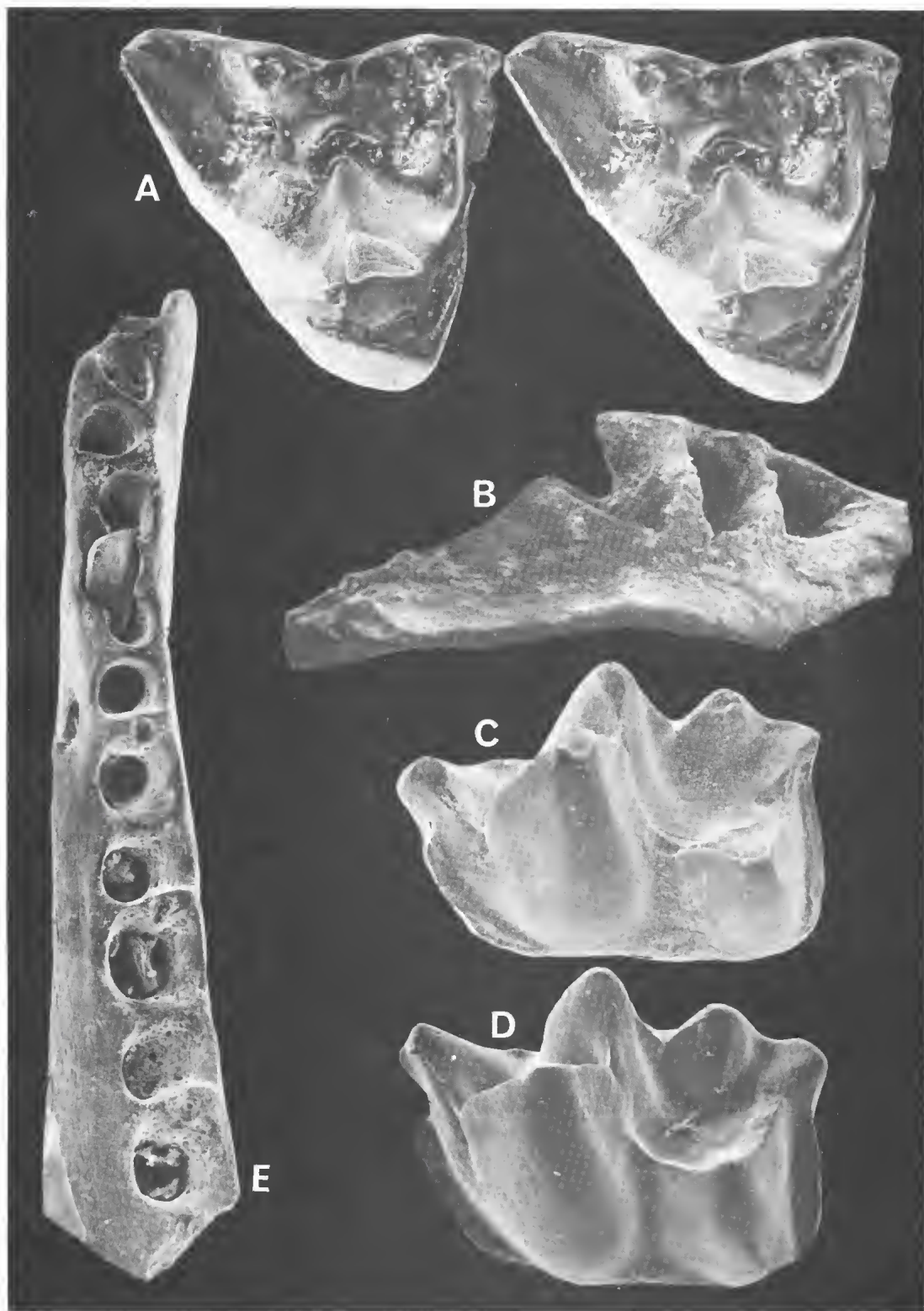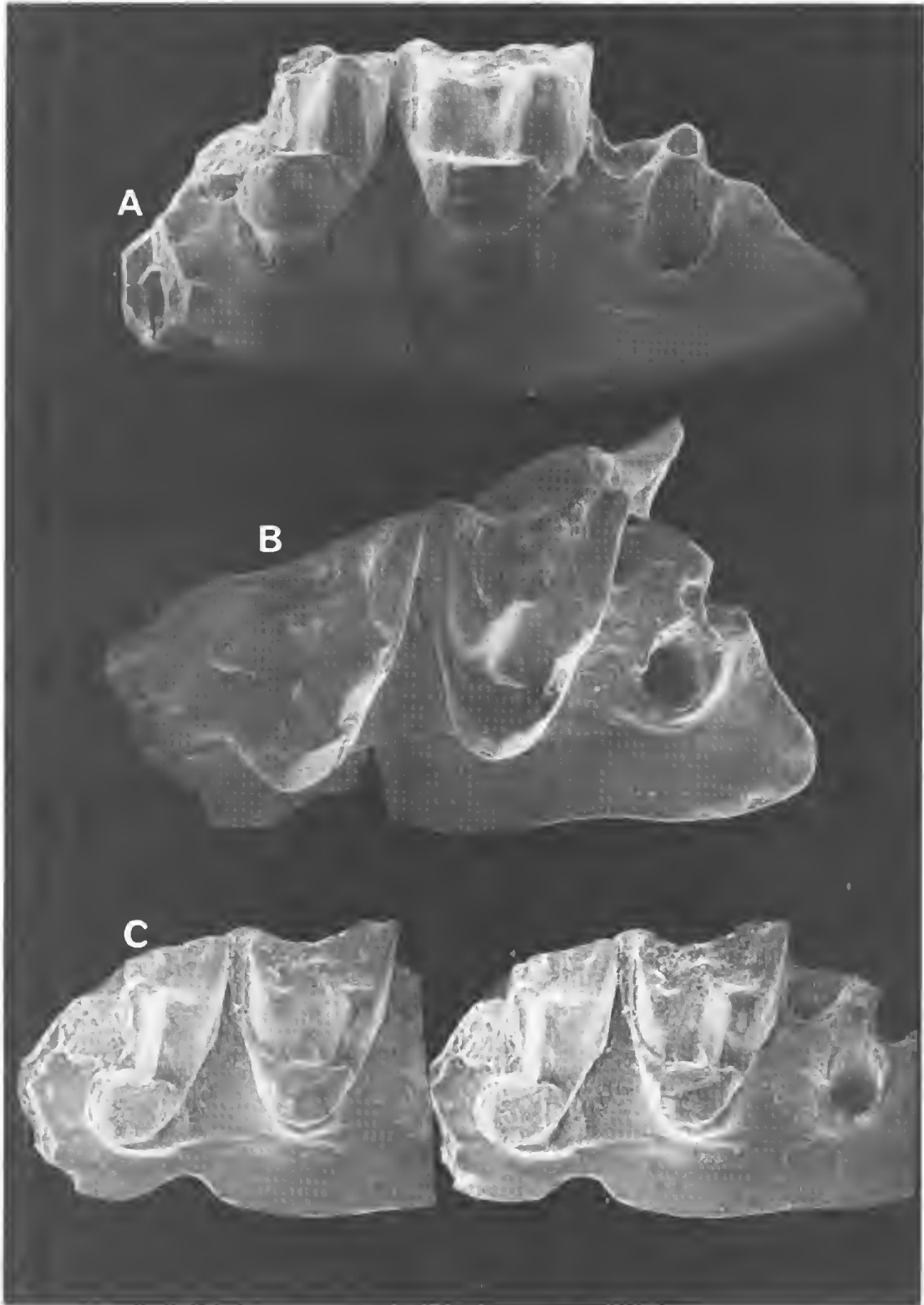
FIG. 7.

FIG. 8.

of stD on M^2-^3; number of cusps in position of stC; presence of stylar crest lingual to stC; less well-developed metaconule; presence of deep pit between bases of paracone and metacone. Lower molars of *Keeuna* differ in having longer metacrista; relatively larger M^3; more lingual intersection of cristid obliqua and trigonid; non-transverse metacristid and hypocristid; large hypoconulid of M_3; antero-posteriorly non-compressed trigonids; relatively unequal heights of the paraconids and metaconids. Differences in position of intersection of cristid obliqua and trigonid in *Ankotarinja* and *Keeuna* not one of kind, but degree, position being relatively more lingual in *Keeuna*.

Other comparisons: No other dasyurids warrant detailed comparisons. Most didelphids reveal fewer similarities, particularly if the referred premaxillary fragment of *Keeuna* does in fact belong to this form. General similarities with Cretaceous didelphines (e.g. some species of *Alphadon* such as *A. rhaister*) include the paracone, which although smaller than the metacone, is not markedly so. Other similarities between *Keeuna* and species of *Alphadon* include relatively reduced stylar cusps (except B), particularly D on M^3 of species such as *A. rhaister* and *A. lulli* Clemens, 1966, and presence of stylar cusp or crest lingual to stC in *A. rhaister*. Marked differences in upper molars of *Keeuna* include much smaller protoand metaconules; less-deeply concave and symmetric ectoloph of M^3; smaller stB; and absent posterior cingulum (present in some species of *Alphadon*). In lower molars, similarities between *Keeuna* and species of *Alphadon* include relatively unreduced trigonid of M_1. Differences in lower molars of *Keeuna* include much smaller paraconid relative to metaconid in M_2-_3 as opposed to specimens referred to species of *Alphadon* (Clemens 1966, Lillegraven 1969).

Compared with holarctic Tertiary didelphines, relative size of paracone in *Keeuna* is similar to condition seen in species of *Peradectes* and *Peratherium*. Other similarities include relatively low stylar cusps; unreduced condition of P_4 (and presumably P^4) and M_1 paraconid; lack of posterior cingulum on upper molars; relatively shallow indentation of ectoloph; extreme buccal position of stylar cusps; and evidently non-transverse orientation of metacristid and hypocristid. Differences in *Keeuna* include relatively larger stylar cusps (particularly D); relatively poorly-developed metaconule; non-pediomyid-like cristid obliqua orientation; relatively taller metaconid and entoconid, and shorter paraconid; and presence of rudimentary buccal cingulum between bases of protoconid and hypoconid. Despite these differences, *Keeuna* more closely resembles these didelphines than any others for which good illustrations or photographs are available.

Close similarities may exist between *Keeuna* and some Paleocene (Riochican) didelphids. Unfortunately very few are known from upper teeth and few are adequately illustrated. As noted above, all modern didelphines examined, and most Tertiary didelphines exhibit a pediomyid type of cristid obliqua, which differs from *Keeuna*. Of all Paleocene forms illustrated by Paula Couto (1952, 1962, 1970) and Simpson (1947), *Mirandatherium* is perhaps most like *Keeuna*. *Keeuna* differs from this didelphid in relatively smaller size of P_4 and presence of buccal cingulum developed between bases of protoconid and hypoconid. Upper molars of *Mirandatherium* are unknown.

Other didelphids do not reveal enough similarities to warrant separate comparisons.

Summary

Teeth of *Keeuna*, although resembling teeth of some Tertiary didelphines such as species of *Peratherium, Peradectes,* and *Mirandatherium,* are broadly similar to teeth of some modern dasyurids such as New Guinean *Antechinus*. In view also of the Australian locality of *Keeuna* it seems most logical to regard this form as a somewhat unusual dasyurid, probably without direct descendants in the modern dasyurid fauna. Resemblances between upper molars of *Ankotarinja* and *Keeuna* further suggest the possibility that these two forms are more closely related to each other than either is to other dasyurids, thereby placing *Keeuna* in a structurally intermediate position between *Ankotarinja* and modern dasyurids.

Discussion of Etadunna marsupicarnivores

Stirton, Tedford, & Miller (1961, p. 35) briefly describe (but not name) another carnivore from the Etadunna Formation. According to their description "The size of the animal is comparable to *Dasyurus quoll* . . . The three

Fig. 8. *A-C*, scanning electron microscope photographs of *Keeuna woodburnei*, F7333, maxillary fragment with partial LM^2, LM^3 and alveoli for LM^4. *C*, stereo photographs.

premolars with gradation in size from P$\frac{4}{1}$ to P$\frac{4}{3}$, and the absence of the metaconid on M$\frac{4}{1}$ suggests that this animal may not be far removed from the ancestry of *Thylacinus*". The author has seen drawings and photographs of this specimen (courtesy Dr W. A. Clemens and Mr C. Campbell) and it is clear that nothing else about the specimen, including the morphology of the upper molars, shows any similarity to *Thylacinus*. On the contrary, it appears to represent another dasyurid lineage (perhaps related to *Dasyurus*) in which metaconid reduction has occurred only on M$\frac{4}{1}$. This unnamed dasyurid and *Keeuna* are the only Etadunna carnivores which can be referred with some confidence to the Dasyuridae.

Ankotarinja is either a didelphid or dasyurid. Compared with known didelphoids, dasyuroids and perameloids, the preserved portions of *Ankotarinja* do not enable confident reference to a particular marsupial family. It is referred to here as ?Dasyuridae.

Ankotarinja and *Keeuna* compared with modern dasyurids, share most dental characters with living New Guinean species of *Neophascogale*, *Phascolosorex*, and *Antechinus*. Similarities with Australian forms are fewer and those that do exist are with forms found in generally non-arid Australian habitats. Broad M$\frac{4}{1}$ talonid, large M$\frac{1}{1}$, narrow and relatively uncrowded premolar row, and large entoconids are characters either lacking or rare in Australian arid-adapted dasyurids. Several authors (e.g. Woodburne 1967, Schodde & Calaby 1972, Stirton, Tedford, & Woodburne 1968) indicate that New Guinea has many mammals (e.g. species of *Dendrolagus* Muller, 1839, *Dorcopsis* Schlegel & Muller, 1839, *Distoechurus* Peters, 1874, *Microperoryctes* Stein, 1932, *Murexia*, *Myoictis*, *Neophascogale* and *Phascolosorex*) from highland rainforest habitats which appear to be structurally ancestral within their respective families.

Evidence for a less-arid central Australia during Ngapakaldi time is reviewed by Stirton, Tedford, & Woodburne (1968). In addition, pollen from the base of the Etadunna Formation, recently obtained from bores in South Australia, has been found to include *Nothofagus* sp. (pers. comm., W. K. Harris, South Australian Department of Mines), a genus of plants presently restricted in the Australian region to the high-rainfall habitats of eastern Australia, New Guinea and New Zealand. Resemblance between Ngapakaldi marsupicarnivores and living New Guinean dasyurids, suggests these living highland New Guinean dasyurids may have avoided certain selective pressures brought to bear on marsupicarnivores living in central Australia, following Ngapakaldi time. These pressures may have included progressive deterioration of climate with increasing aridity. Elsewhere, as part of revision of the dasyurid genus *Sminthopsis*, the author has given evidence for believing that several Australian dasyurid lineages underwent arid-adaptation. Arid-adapted forms now dominate the majority of Australia and are in clear contrast to the marsupicarnivores of the Ngapakaldi local fauna described here.

References

ARCHER, M. (1974).—The development of the cheek-teeth in *Antechinus flavipes* (Marsupialia, Dasyuridae). *J. R. Soc. West. Aust.* **57**, 54-63.

ARCHER, M. (1975a).—The development of premolar and molar crowns of *Antechinus flavipes* (Marsupialia, Dasyuridae) and the significance of cusp ontogeny in mammalian teeth. *J. R. Soc. West. Aust.* **57**, 118-125.

ARCHER, M. (1975b).—*Ningaui*, a new genus of tiny dasyurids (marsupialia) and two new species, from arid Western Australia, *N. timealeyi* and *N. ridei*. *Mem. Qd Mus.* **17**, 27-29.

ARCHER, M. (1975c).—Abnormal dental development and its significance in dasyurids and other marsupials. *Mem. Qd Mus.* **17**, 251-265.

ARCHER, M. (1976a).—Revision of the marsupial dasyurid genus *Planigale* Troughton. *Mem. Qd Mus.*, in press.

ARCHER, M. (1976b).—The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhyaenids (Marsupicarnivora) and peramelids (Peramelina). *Aust. J. Zool., Suppl. Series*, in press.

BENSLEY, B. A. (1903).—On the evolution of the Australian Marsupialia; with remarks on the relationships of the marsupials in general. *Trans. Linn. Soc. Lond. (Zool.)* **9**, 83-217.

CLEMENS, W. A. (1966).—Fossil mammals of the Type Lance Formation Wyoming Part II. Marsupialia. *Bull. Dep. Geol. Univ. Calif.* **62**, 1-122.

CLEMENS, W. A. (1973).—Fossil mammals of the Type Lance Formation Wyoming Part III. Eutheria and summary. *Bull. Dep. Geol. Univ. Calif.* **94**, 1-102.

COLLINS, L. R. (1974).—"Monotremes and marsupials." (Smithsonian: Washington.)

GRAHAM, S. F., & RIDE, W. D. L. (1967).—Infraclass Metatheria. *In* "The Fossil Record". (Geol. Soc. Lond.: London.)

LAURIE, E. M. O., & HILL, J. E. (1954).—"List of land mammals of New Guinea, Celebes and adjacent islands 1758-1952." (Tonbridge Printers: Tonbridge.)

LILLEGRAVEN, J. A. (1969).—Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *Paleont. Contr. Univ. Kans. Article* **50** (Vertebrata 12), 1-122.

PAULA COUTO, C. DE (1952).—Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Didelphidae. *Amer. Mus. Novit.* **1567**, 1-26.

PAULA COUTO, C. DE (1962).—Didelfideos fossiles del Paleoceno de Brasil. *Ciencias Zoológicas* **8**, 135-166.

PAULA COUTO, C. DE (1970).—News on the fossil marsupials from the Riochican of Brazil. *An. Acad. brasil. Cienc.* **42**, 19-34.

REIG, O. A. (1957).—Sobre la posicion sistematica de "*Zygolestes paranensis*" Amegh. y de "*Zygolestes entrerrianus*" Amegh. con una reconsideracion de la edad y correlacion del "Mesopotamiense". *Holmbergia* **5**, 209-226.

RIDE, W. D. L. (1964).—*Antechinus rosamondae*, a new species of dasyurid marsupial from the Pilbara District of Western Australia: with remarks on the classification of *Antechinus*. *W. Aust. Nat.* **9**, 58-65.

RIDE, W. D. L. (1970).—"A guide to the native mammals of Australia." (Oxford Univ. Pr.: Melbourne.)

ROBINSON, R. (1966).—"Aboriginal myths and legends." (Sun Books: Melbourne.)

SCHODDE, R., & CALABY, J. H. (1972).—The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. In D. Walker (Ed.) "Bridge and barrier: the natural and cultural history of Torres Strait." (Aust. Nat. Univ. publ., B6/3(1972); Canberra.)

SIGE, B. (1972).—La faunule de mammiferes du Crétacé supérieur de Laguno Umayo (Andes péruviennes). *Bull. Mus. natn., Hist. nat.* (3) **99**, 375-405.

SIMPSON, G. G. (1928).—American Eocene didelphids. *Amer. Mus. Novit.* **307**, 1-7.

SIMPSON, G. G. (1929).—American Mesozoic Mammalia. *Mem. Peabody Mus., Yale* **3**, 1-171.

SIMPSON, G. G. (1941).—The affinities of the Borhyaenidae. *Amer. Mus. Novit.* **118**, 1-6.

SIMPSON, G. G. (1945).—The principles of classification and a classification of mammals. *Bull. Amer. Mus. nat. Hist.* **85**, i-xvi, 1-339.

SIMPSON, G. G. (1947).—A new Eocene marsupial from Brazil. *Amer. Mus. Novit.* **1357**, 1-7.

SIMPSON, G. G. (1948).—The beginning of the age of mammals in South America Part I. Introduction. Systematics: Marsupialia, Edentata, Condylarthra, Litopterna, and Notioprogonia. *Bull. Amer. Mus. nat. Hist.* **91**, 1-232.

SINCLAIR, W. J. (1906).—Mammalia of the Santa Cruz beds. Marsupialia. *Rep. Princeton Exped. Patagonia* **4**, 333-460.

SMITH, J. (1880).—"The Booandik Tribe of South Australian Aborigines: a sketch of their habits, customs, legends, and language." (Govt. Printer: Adelaide.)

STIRTON, R. A., TEDFORD, R. H., & MILLER, A. H. (1961).—Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. *Rec. S. Aust. Mus.* **14**, 19-61.

STIRTON, R. A., TEDFORD, R. H., & WOODBURNE, M. O. (1968).—Australian Tertiary deposits containing terrestrial mammals. *Bull. Dep. Geol. Univ. Calif.* **77**, 1-30.

THOMAS, O. (1887).—On the homologies and sucession of the teeth in the Dasyuridae. *Phil. Trans. R. Soc.* **178**, 443-462.

WOODBURNE, M. O. (1967).—The Alcoota Fauna, Central Australia: an integrated paleontological and geological study. *Bur. Min. Resour. Aust. Bull.* **87**, 1-187.

WOODS, H. E. (1924).—The position of the "sparassodonts"; with notes on the relationships and history of the Marsupialia. *Bull. Amer. Mus. Nat. Hist.* **51**, 77-101.